

A new ghost shrimp of the genus *Lepidophthalmus* from the Pacific coast of Colombia (Decapoda: Thalassinidea: Callinassidae)

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Abstract.—*Lepidophthalmus rafai* is described from an intertidal shoreline in the vicinity of Buenaventura, Pacific coast of Colombia, South America. While recent collecting has uncovered populations assignable to described and undescribed species of the genus in intertidal habitats of the tropical eastern Pacific, most of these are forms with a ventrally plated or armed abdomen and a strongly trilobate posterior margin on the telson, features that suggest close relationship to *L. bocourti* (A. Milne Edwards) or *L. eiseni* Holmes. The new species is smaller in size than its congeners and is the most southerly distributed species of the genus known from the eastern Pacific. It lacks conspicuous sclerotized plates on ventral surfaces of the abdomen, a feature that it shares with a pair of antitropically distributed species in the western Atlantic. The two Atlantic forms, and the herein described new Pacific species, may have diverged from common stock partitioned by closing of the Panamanian Isthmus. The occurrence of *L. rafai* in a perturbed, hypoxic estuarine habitat is consistent with tolerances and adaptations documented previously for other species of the genus.

Previous reports of the ghost shrimp genus *Lepidophthalmus* Holmes, 1904, from Colombia have included materials of an endemic species, *L. sinuensis* Lemaitre & Rodrigues, 1991, limited in distribution to a restricted area of the Caribbean coast (Lemaitre & Rodrigues 1991, Felder et al. 1995, Nates et al. 1997), and materials assigned to *L. bocourti* (A. Milne Edwards, 1870) from Malaga Bay and Gorgona island on the Pacific coast (Lemaitre & Ramos 1992, Lemaitre & Alvarez-León 1992). All of these specimens exhibit a characteristic armor of sclerotized plates on ventral surfaces of the anterior abdominal somites (Felder & Manning 1997) and/or have a strongly trilobate posterior margin on the telson.

In the course of our ongoing studies of *Lepidophthalmus* spp. in the eastern Pacific,

which includes populations from Mexico to Colombia, we have found that previously unrecognized variation in pattern and sculpture of ventral sclerites and other structures may be of value in distinction of *L. bocourti*, *L. eiseni* Holmes, 1904, and other regional forms, most of which appear to be closely related to one another. These, including the aforementioned materials of *L. bocourti* from Colombia and other eastern Pacific materials previously reported as either *L. bocourti* or *L. eiseni* will be treated together in a forthcoming revision. However, a single eastern Pacific lot of five specimens from the coast of Colombia lacks both abdominal sclerotization and a strongly trilobate posterior margin on the telson. On the basis of these unique specimens, we herein describe a new species and suggest it to represent the first known east-

ern Pacific cognate of two similarly unarmed western Atlantic forms, *L. louisianensis* (Schmitt, 1935) and *L. siriboia* Felder & Rodrigues, 1993.

As members of the genus *Lepidophthalmus* are known to exhibit an abbreviated larval life history with limited planktonic dispersal (Felder et al. 1991, Manning & Felder 1991, Nates et al. 1997), it is perhaps not surprising that regionally endemic populations and undescribed species continue to be found in the course of sampling infauna from isolated river mouths and coastal estuaries of the tropical Americas. However, throughout this region, rapidly expanding maricultural, urban and port development activities now threaten to alter distributions of these populations by way of both habitat modification and cross-seeding of regionally endemic forms. Given their at least short term negative impacts on shrimp production (Felder et al. 1995, Nates & Felder 1998), opportunistic species such as *L. sinuensis* that invade and densely colonize penaeid culture ponds in tropical estuaries are considered pest species for which extermination and control measures are being sought. The above issues compel urgency for thorough understanding of diversity, systematic relationships and ranges for this taxocene, both to gain zoogeographic insights from natural distributions and to predict impacts of regional anthropogenic developments.

Material examined is listed by location followed by date, collector, number of specimens by sex, size in parenthesis, and museum number. Size is expressed as postorbital carapace length (CL) or postorbital total length with the abdomen extended (TL) and measured in millimeters (mm). The holotype and paratype females of *L. rafai* have been deposited in the National Museum of Natural History Smithsonian Institution, Washington, D.C. (USNM); the paratype male has been deposited in crustacean collections of the Museo de Historia Natural del Instituto de Ciencias Naturales de la Universidad Nacional de Colombia,

Santa Fe de Bogotá (ICN-MNH-Cr). Holdings of the USNM and The University of Southwestern Louisiana Zoological Collections (USLZ) were the source for comparative materials of *L. louisianensis* from the Gulf of Mexico and *L. siriboia* from Brazil, as well as most examples of congeneric populations from the eastern Pacific. Comparison to the male holotype of *L. bocourti* was made while that specimen, MNHN Th. 64, was on loan to us from the Muséum National d'Histoire Naturelle, Paris. Comparison to what are possibly the eastern Pacific type specimens of *L. eiseni* was based upon examination of cataloged lot number MCZ 4370, provided on loan from the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; compelling evidence for these being the probable types was presented by Biffar (1972:69-70).

Systematics

Lepidophthalmus Holmes, 1904

Diagnosis.—See Manning & Felder, 1991.

Lepidophthalmus rafai, new species

Figs. 1a-h, 2a-h, 3a-i

Material examined.—Holotype: Beach at Playa Basura, Bahía de Buenaventura, Pacific coast of Colombia, 3°53'48"N, 77°05'12"W, 18 Oct 1991, coll. J. Tovar, 1 male (CL 6.0 mm), USNM 260797. Paratypes: Same location, date, coll., 1 male (CL 7.2 mm), ICN-MNH-Cr 1678; 3 females (CL 5.1, 6.6, 6.8 mm) USNM 259407.

Diagnosis.—Rostrum acute, flanked by low angular shoulders lateral to eyestalks. Branchiostegite with sclerotized boss in anterior 1/5. Ventral margin of cheliped merus strongly bicarinate. Dactyl of major chela in male with subrectangular prehensile tooth near 2/5 length, separated by notch from broad, subtriangular distal tooth. Second abdominal somite lacking sclerotized

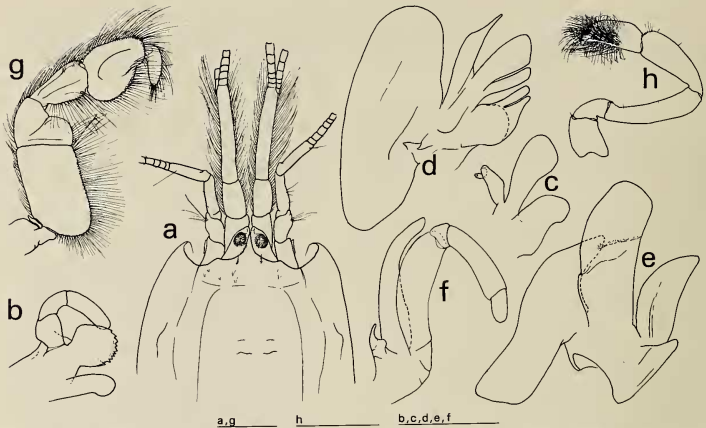


Fig. 1. *Lepidophthalmus rafai*, new species, holotype male from Bahía de Buenaventura, Pacific coast of Colombia, USNM 260797 (CL 6.0 mm): a, anterior carapace, eyestalks and antennae, dorsal surface; b, right mandible and paragnath, external surface, setation not shown; c, right first maxilla, external surface, setation not shown; d, right second maxilla, external surface, setation not shown; e, right first maxilliped, external surface, setation not shown; f, right second maxilliped, external surface, setation not shown; g, right third maxilliped, external surface; h, right fifth pereopod, external surface. Scale lines indicate 1.0 mm.

ventromedial plate. Appendix interna of male second pleopod small, not reaching to end of endopod. Second through fifth pleopods lacking distolateral spine on anterior surface of basis. Telson broad, subovoid, posterior margin not strongly trilobate. Uropodal endopod broadly suboval to sub-rhomboid, about 1.5 times longer than broad.

Description.—Frontal margin of carapace with acute, narrow rostral spine flanked laterally by low, weakly angular shoulders (Fig. 1a), apices of which are immediately lateral to eyestalks; rostral spine directed anteriorly, extending about $\frac{3}{4}$ length of eyestalks in dorsal view, base of spine ventrally with tuft of setae, longest of which extend anteriorly between eyestalks beyond cornea. Carapace anterior to dorsal oval with several pairs of short setose punctae on either side of midline and scattered smaller punctae laterally, some longer setae plumose; dorsal oval well defined, smooth,

usually with pair of widely separated setal punctae anterior to midlength, length of oval slightly more than $\frac{1}{10}$ of postrostral carapace length; marginal suture of oval diminished at anterior midline, stronger and with sclerotized articulation to cardiac region at posterior midline; branchiostegite with low, sclerotized boss in anterior $\frac{1}{2}$.

Eyestalks subtriangular in dorsal view, reaching to or beyond $\frac{3}{4}$ length of basal antennal article; anterolateral margins tapered to thin, arcuate flange, dorsomesial margin thickened to form low marginal ridge or poorly defined tubercle in distal $\frac{3}{4}$, ridge extending to blunt terminal protuberance of eyestalk (Fig. 1a); distinct, pigmented cornea centered on dorsal surface, area of pigmentation often broader than faceted surface. Antennular peduncle longer and slightly heavier than antennal peduncle; basal article dorsally invaginated to form statocyst occluded by setae, overlain by eyestalk; length of second article subequal to

that of basal article, third article about 2.5 times length of second; second and third articles with dense, ventromesial and ventrolateral rows of long, ventrally directed setae; rami of flagellum slightly longer than third article of peduncle, ventral ramus slightly longer, narrower, and with much denser, longer setation than dorsal ramus, subterminal articles of dorsal ramus much broader than those of ventral ramus and fringed with short, dense ventral setae. Antennal peduncle reaching barely beyond midlength of third article of antennular peduncle; basal article with dorsolateral carina strong proximally, forming lip above excretory pore, ventrally with setose distomesial protuberance; second article with distal field of long setae on lateral boss; third article elongate, slightly shorter than combined lengths of first two, slightly shorter than fourth, laterally with few long setae; fourth article narrower than others, setation limited to few long subterminal setae; flagellum with sparse short setae, about 3 times length of antennular flagella.

Mandible (Fig. 1b) with large, setose, 3-segmented palp, elongate third article of palp compressed distally, becoming subspatulate, weakly truncate terminally; gnathal lobe of mandible with weakly angular distolateral shoulder, incisor process with well-defined corneous teeth on cutting margin, concave internal surface with lip giving rise to molar process with a corneous tooth proximal and internal to incisor teeth; thin, rounded paragnath set against proximal convex surface of molar process. First maxilla (Fig. 1c) with endopodal palp narrow, terminal article deflected at poorly defined articulation; proximal endite with mesial margin sinuous, distal endite elongate, terminally broadened and with dense spini-form setation; exopodite low, rounded. Second maxilla (Fig. 1d) with margins setose, endopod narrowed terminally, first and second endites each longitudinally subdivided, exopod forming large, ovoid scaphognathite. First maxilliped (Fig. 1e) with margins setose, endopod rudimentary, overlain by

distal endite; proximal endite angular, coarsely setose distomesial corner directed to internal side of endite; distal endite sub-ovoid, narrowed distally, proximal $\frac{2}{5}$ of external surface with longitudinal carina, mesial half densely setose; exopod incompletely divided by oblique suture, lateral margin near midlength offset to form slightly produced corner at intersection with suture, mesial margin with comb of close-set long setae, external face with dense field of mesially directed setae distal to oblique suture; epipod large, broad, anterior end strongly tapered. Second maxilliped (Fig. 1f) with margins setose, endopodal merus and propodus arcuate, both slightly broader distally than proximally, flexor margin of merus with comb of long setae, internal surface produced distally to form rounded lobe extending over internal surface of short carpus; merus length 3.0–3.5 times width; propodus length about $\frac{2}{3}$ length of merus, longest setae originating on extensor margin and distal half of external surface; dactylus almost twice as long as broad, terminally rounded, distal half bearing stiff setae; exopod narrow over most of length, width at $\frac{3}{4}$ length about $\frac{1}{2}$ of width at $\frac{1}{4}$ length, overreaching endopodal merus, arcuate, terminally rounded; bilobed epipod with broad basal lobe, narrow tapered, weakly hooked distal lobe. Third maxilliped (Fig. 1g) with small, naked, terminally acute, rudimentary exopod and large setose endopod; endopodal ischium subrectangular, length less than 2 times width, internal surface with weak, unarmed longitudinal carina, strongest proximally; merus subtriangular, broader than long, mesial margin forming a distinct rounded lobe; carpus subtriangular, longer than broad; terminal articles twisted, directing tip of dactyl toward posterior; propodus large, subovoid, slightly longer than broad; dactylus narrow, arcuate proximally, long setae of extensor and distal margins including a few long stiff bristles at terminus.

Branchial formula as reported for congeners (Lemaitre & Rodrigues 1991:625,

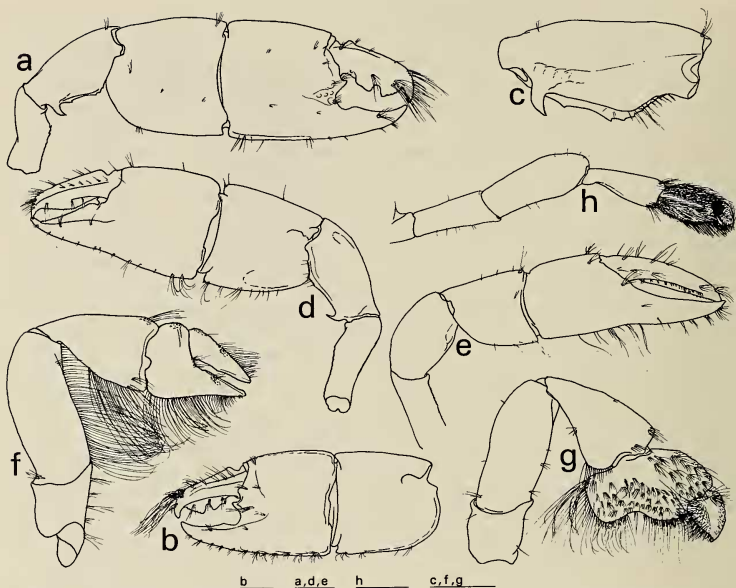


Fig. 2. *Lepidophthalmus rafai*, new species, type specimens from Bahía de Buenaventura, Pacific coast of Colombia. Holotype male, USNM 260797 (CL 6.0 mm): a, major cheliped, external surface; b, major chela, internal surface; c, merus of major chela, external surface; f, right third pereiopod, external surface. Paratype female, USNM 259407 (CL 6.6 mm): d, major chela, internal surface; h, right fourth pereiopod, external surface. Paratype male, ICN-MNH-Cr 1678 (CL 7.2 mm): e, minor cheliped, external surface. Scale lines indicate 1.0 mm.

Felder & Rodrigues 1993:363, 369–370); endopods and epipods as described above, branchiae limited to single rudimentary arthrobranch on second maxilliped, pair of arthrobranches on third maxilliped, and pair of arthrobranches on each of the first through fourth pereiopods.

Major cheliped located on either right or left side of body, shape and ornamentation sexually dimorphic. Major cheliped of male (Fig. 2a–c) massive, more strongly armed than that of female; ischium slender, superior margin sinuous, row of small denticles on proximal $\frac{2}{3}$ of inferior (flexor) margin, row usually terminated distally with a few stronger, sometimes hooked teeth; merus

(Fig. 2c) with broad, shallow notch in proximal $\frac{1}{5}$ of superior margin, inferior (flexor) margin subangular, with strong proximal arthrohook at base of bicarinate keel, external carina unarmed, internal carina forming inferior margin bearing (usually 4–6) small distally directed or slightly hooked denticles, most of which are positioned near or distal to angular bend of inferior margin; external surface of article weakly eroded above proximal hook; carpus broad, subquadrate, superior and inferior margins keeled, near parallel to weakly convergent in distal half, terminated distally in angular corners. Propodus of male major chela broad, heavy, length of fixed finger markedly exceeding

$\frac{1}{2}$ length of palm; inner surface of palm (Fig. 2b) smooth proximally, with few setose punctae along unarmed carina extending onto fixed finger; outer surface (Fig. 2a) with short unarmed longitudinal carina and adjacent weakly tuberculate depression extending proximally from gape of fingers; distinct keel of superior propodal margin terminating just short of distal articulation with dactylus, keel of inferior margin distinct proximally, extending onto fixed finger, distally diminished and overlain by setose punctae; subtriangular, superodistally directed tooth at proximal end of gape, tooth undercut by broadly U-shaped notch at base of fixed finger, notch terminated distally by low prehensile tooth near $\frac{1}{2}$ length of fixed finger; fixed finger with well defined separation of inner and outer prehensile margins, inner margin unarmed; dactylus with hooked tip, superior margin with erect tubercle at proximal end, inferior surface with unarmed, weakly developed inner margin, outer prehensile margin usually with two large, variously subdivided prehensile teeth, subrectangular proximal tooth centered near $\frac{2}{5}$ length, separated by a U-shaped notch from broad, often subtriangular distal tooth, distal shoulder of which is typically cut into a series of small teeth running distally.

Major cheliped of female less massive (Fig. 2d), less strongly armed than that of male; merus with weak distal dentition on outer inferior carina than in male; outer prehensile margins of fixed finger and dactylus weakly serrate, dactyl relatively less massive and fixed finger broader than in males, notch at base of fixed finger very narrow; superior and inferior margins of propodus distinctly converging distally, inferior margin broadly sinuous; when fingers closed, dactyl usually overreaching fixed finger, tips slightly crossing, gape filled except for deepest part of notch at base of fixed finger.

Minor cheliped (Fig. 2e) sparsely armed; ischium with row of minute denticles or tubercles on most of flexor margin; merus unarmed; carpus with angular distal corners.

Minor chela with fixed finger bearing tufts of short setae on proximal $\frac{2}{3}$ of outer prehensile margin, prehensile surface lacking excavate area of dense setation, gape between fingers narrow; dactylus with inferior (prehensile) surface mostly unarmed over proximal $\frac{2}{3}$, subterminally with minute corneous serrations on outer prehensile margin, fingers terminating in corneous tips.

Second pereopod (Fig. 2f) chelate, flexor margins of merus and distal $\frac{2}{3}$ of carpus lined with evenly spaced long setae, inferior margin of propodus weakly concave, with setae long proximally, reduced in length to short bristles distally, subterminally with separated minute tuft of short, stiff bristles; middle $\frac{1}{3}$ of fixed finger with patch of short, stiff bristles just outside prehensile margin; tips and prehensile margins of both fingers corneous; granulated superior margin of dactylus with stiff, arched bristles reduced in length distally. Third pereopod (Fig. 2g) merus length about 2.4 times width; propodus with inferodistal margin bilobate and separated from articulation of dactylus by external furrow, lobes demarcated by furrows on internal surface, distal margins of both lobes with bristles longest on weakly scalloped margins, those in distal half of upper lobe partially concealing 1–2 prominent, corneous, distally directed teeth arising from margin; longest setae on inferior margin of lower lobe, patterned tufts of lighter setae on outer face of article; dactylus subtriangular, superior margin granulated, weakly sinuous, narrowed distally to short ventrolaterally directed corneous tooth, outer surface with row of stiff bristles lining inferior margin, fields of finer setae above. Fourth pereopod (Fig. 2h) weakly subchelate, inferodistal process of propodus (= fixed finger) a weak angular lobe extended distally about $\frac{1}{3}$ length of dactylus, lower margin of lobe with usually 3–4, well developed, articulated corneous spines, often obscured by dense brush of stiff setae, dactylus subtriangular, superior margin arched, narrowed distally to short ventrolaterally directed corneous tooth. Fifth pe-

reipod (Fig. 1h) minutely chelate, opposable surface of minute dactylus spooned, terminally rounded, cupping short blunt fixed finger to form beak-like chela obscured by dense fields of setation on distal $\frac{2}{3}$ of propodus and superior surface of dactylus.

Abdominal somites mostly smooth dorsally, glabrous; first abdominal tergite thin and translucent dorsally, enclosed anteriorly and laterally by narrow marginal sclerite, arms of which diverge toward posterior of somite; marginal sclerite articulated anterolaterally to narrow arched lateral carina, extending anteroventrally toward thorax; second tergite poorly sclerotized, small tuft of long setae at posterolateral extreme; third-fifth tergites each encompassing a finely setose, lateral, membranous subcircular or suboval area below a weak posterolateral suture, that of the third tergite larger, more circular and more posterolaterally positioned than in the fourth and fifth tergites; sixth tergite (Fig. 3i) with 2 posterolateral lines of short setae anterior to posterolateral groove from which transverse suture originates, longest line adjacent and subparallel to transverse suture, weakly defined posterior suture directed anteriorly, tufts of stiff setae on posterolateral corners, and usually as 4 short lines or tufts of stiff setae on posterior margin. Ventral surfaces of abdominal somites without conspicuous armor of plates or tubercles.

First pleopod of male and female uniramous, composed of 2 articles; in male, weak suture separating articles (Fig. 3a-c), appendage length about $\frac{1}{2}$ that of second pleopod, proximal article less than 2 times length of terminal article, terminal article flattened, bifurcate, anterolaterally directed tip with several terminal denticles, both tips with long subterminal setae (bases of which are densely fouled by small fungal hyphae in holotype); in female (Fig. 3d), extended length subequal to that of second pleopod, proximal article slightly shorter and heavier than terminal article, terminal article narrowed to spatulate blade beyond midlength,

both articles bearing long setae. Second pleopod of male and female biramous, with appendix interna on endopod; appendix interna of male (Fig. 3e, f) small, not reaching to tip of endopod, terminally subacute, subterminal shoulder with field of minute, rudimentary hooked setae (fouled by longer fungal hyphae in holotype); in female (Fig. 3g), both rami setose, appendix interna small, slightly elongate. Basis of second through fifth pleopods with, at most, a low tubercle or tooth on anterior surface at articulation with exopod. Third to fifth pleopod pairs forming large, posteriorly cupped fans when cross-linked by hooked setae of appendices internae on opposed margins of endopods; endopod of each subtriangular (Fig. 3h) articulation of stubby appendix interna embedded into mesial margin. Telson (Fig. 3i) broad, subovoid, width about 1.4 times length, posterior margin weakly to indiscernibly trilobate, median lobe most pronounced; dorsal surface usually with pair of setal tufts near midlength; lateral margins typically with pair of setal tufts near midlength, posterior margin with distinct tuft on each of weak posterolateral lobes. Uropod (Fig. 3i) with short, angular, posteriorly directed prominence on protopod and short, posteromesially directed tooth on proximal article of exopod, both abutting or overreaching anterior margin of extended endopod; endopod broadly ovoid to subrhomboidal, about 1.5 times longer than broad, rounded terminus bearing marginal fringe of long setae, posteromesial margin with isolated tufts of setae; exopod with anterodorsal plate falling well short of distal endopodal margin, posterodistal edge of plate with short, thick, spiniform setae grading to thinner, dense, elongate setae of exopod margin; distal margin of exopod with dense fringe of setation, longest posteriorly.

Size.—Apparently smaller than known congeners, on the basis of present materials which appear to be mature or nearly so. In postorbital length, measured after preservation, the largest male is CL 7.2 mm, TL 30.5 mm; the largest female CL 6.8 mm,

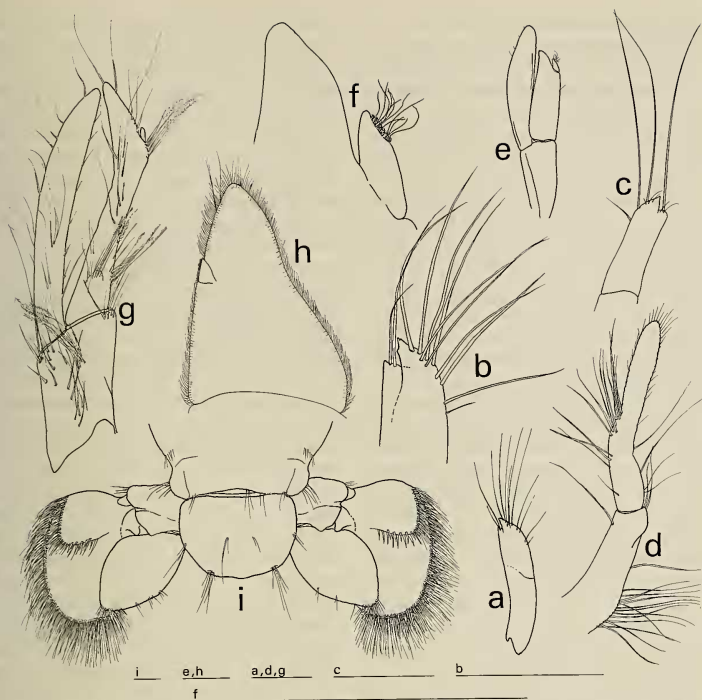


Fig. 3. *Lepidophthalmus rafai*, new species, type specimens from Bahía de Buenaventura, Pacific coast of Colombia. Holotype male, USNM 260797 (CL 6.0 mm): a, right first pleopod (gonopod), external surface; b, right first pleopod (gonopod), terminus; e, right second pleopod, posterior surface; f, right second pleopod, appendix interna and terminus of endopod; i, sixth abdominal somite, telson and uropods, dorsal surface. Paratype male, ICN-MNH-Cr 1678 (CL 7.2 mm): c, left first pleopod (gonopod), external surface. Paratype female, USNM 259407 (CL 6.6 mm): d, right first pleopod, external surface; g, right second pleopod, posterior surface; h, endopod of right third pleopod, anterior surface. Scale lines indicate 0.5 mm.

TL 30.0 mm. Egg size is unknown, as no ovigerous specimens have been collected to date. Sampling conducted by J. Tovar at the type locality was limited to the upper 20 cm of sediment (G. E. Ramos, Universidad del Valle, Cali, Colombia, pers. comm.), and larger individuals of the population thus may not have been captured.

Habitat.—Known from only the type locality at Playa Basura (meaning “Garbage

Beach” in English), Bahía de Buenaventura, Pacific coast of Colombia. According to notes furnished by G. E. Ramos (Universidad del Valle, Cali, Colombia, pers. comm.), the low-gradient intertidal habitat is very muddy and heavily contaminated by organic material from a nearby sewage outfall (“aguas negras” in Spanish) from the nearby city of Buenaventura. The area has also been impacted previously by cutting of

mangroves and dredging of a port for tourist traffic. Subsequently, walls to retard erosion have been constructed along 300–400 m of coastline here, and sandy materials have begun to accrue which have somewhat indurated selected areas of the muddy substrate.

Etymology.—The species is named in recognition of many contributions by our friend and colleague, Rafael Lemaitre, to the study of decapod crustaceans. Known to many friends by the nickname “Rafa”, Dr. Lemaitre’s extensive publications and generous assistance to colleagues have substantially improved systematic understanding of many decapod assemblages, in both his native Colombia and abroad.

Remarks.—*Lepidophthalmus rafai* differs from known populations of congeneric eastern Pacific species in lacking a strongly trilobate posterior margin on the telson, such as was figured by Bott (1955: fig. 7g) and Biffar (1972: fig. 17a). In addition it lacks well developed sclerotized plating on membranous ventral surfaces of the anterior abdominal somites, which is particularly evident in the absence of a large ventromedial plate on the second abdominal somite. Such plates, varying from subquadrate to near hourglass in shape, are conspicuously evident in the very large (CL 24.5 mm) male holotype specimen of *L. bocourti* (A. Milne Edwards, 1870) (MNHN Th. 64) from “La Union” (likely the shores of Golfo de Fonseca, El Salvador) and in the comparably large (CL 25.0–26.0 mm) male and female probable type specimens of *L. eiseni* Holmes, 1904 (lot number MCZ 4370) from the southern tip of the Baja California peninsula. This ventral abdominal plating was also perviously described in part for specimens of *L. eiseni* reported from El Salvador (Holthuis 1954:12–13).

Such plates and other extensive ventral sclerotization are evident on close inspection of recently collected smaller individuals that we assign to either of the aforementioned species, including several specimens which are comparable in size to the

type series of *L. rafai*. Additionally, the first through fifth pleopods in *L. rafai* lack a distolateral spine on the anterior surface of the basis, a characteristic feature of adults and juveniles in both sexes of *L. bocourti*.

Provided that presently available small specimens of *L. rafai* accurately represent the approximate mature size and configuration of secondary sexual structures, males of this new species may also differ from both *L. bocourti* and *L. eiseni*, as well as from other undescribed eastern Pacific specimens of the genus available to us, in the diminutive size of the appendix interna on the second pleopod. In both *L. bocourti* and *L. eiseni*, the appendix interna of this appendage is usually comparable in size to the terminal lobe of the endopod and is adorned with elongate terminal setae, much as in the Caribbean species *L. jamaicense* (Schmitt 1935) (Felder & Manning 1997: fig. 1h). However, at sizes comparable to our small specimens of *L. rafai*, specimens of *L. bocourti* and *L. eiseni* do not always exhibit secondary sexual characters of mature form.

Over the full size range of available specimens, including sizes comparable to the types of *L. rafai*, specimens of both *L. bocourti* and *L. eiseni* appear to have smaller, narrower uropodal endopods (relative to exopods) than do specimens of *L. rafai*. In addition, *L. rafai* has a very strongly developed bicarinate, rather than weakly bicarinate or single, ventral margin on the merus of the major cheliped. While such bicarination of the meral margin is also evident in type materials of *L. eiseni* and most other congeneric eastern Pacific materials that we have seen (the chela is lacking in the type of *L. bocourti*), it is often poorly defined or limited to the anterior or posterior half of the ventral margin, especially in specimens comparably sized to those of *L. rafai*.

Absence of the ventral abdominal plating also distinguishes *L. rafai* from the Caribbean species *L. jamaicense*, *L. sinuensis*, *L. richardi* Felder & Manning, 1997, and an undescribed population from the south-

western Gulf of Mexico. However, it shares the absence of such armor with at least *L. louisianensis* from the northern Gulf of Mexico and *L. siriboia* from Brazil, antitropically distributed western Atlantic species that closely resemble *L. rafai* and perhaps shared a common lineage with this eastern Pacific form preceding their separation from it by the Panamanian Isthmus. *L. rafai* further resembles *L. siriboia* in having a distinct bicarinate ventral margin on the merus of the major cheliped, forming a longitudinal groove between the carinae. It differs from *L. siriboia* and many other congeners in sculpture of the major chela, the dactylar dentition of which most resembles that of *L. louisianensis*, and in having a pronounced mesial lobe on the merus on the third maxilliped.

The materials of *L. rafai* were discovered by J. Tovar in the course of a search for bioindicator species in a heavily contaminated environment. It is noteworthy that other members of the genus are also known to flourish in such richly organic and hypoxic environments (Felder 1979, Felder et al. 1995, Nates & Felder 1998), where they apparently tolerate or perhaps derive some benefit from elevated concentrations of reduced minerals or nutrients, sometimes to the apparent detriment of animals in the overlying water layer (Nates & Felder 1998). Recent evidence of an intrinsic ability for sulfide metabolism in several eastern Atlantic thalassinid genera (*Calocaris*, *Callianassa*, and *Jaxea*), and the suggestion that this mechanism may provide an ancillary energy source for those burrowing animals (Johns et al. 1997) raises the likelihood that such pathways could also operate in members of *Lepidophthalmus*, including *L. rafai*. We are aware of no other callinassid genus that so readily invades, colonizes, and deeply burrows into organically rich estuarine sediments, including those that are strongly hypoxic and sometimes sulfidic. Much as eastern Atlantic mudshrimp are among the few species to survive in sediments of sea lochs where place-

ment of commercial fish cages has intensified hypoxia and hypercapnia (Atkinson 1987), members of the genus *Lepidophthalmus* can be expected to sometimes survive and perhaps thrive as a dominant macrofaunal form in those coastal American habitats subject to organic and nutrient loading from sewage effluents, maricultural operations, and other sources of eutrophication (Felder & Griffis 1994, Nates & Felder 1998).

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